THE DIET OF THE EARLY TOARCIAN AMMONITE *HARPOCERAS FALCIFERUM*

by MANFRED JÄGER *and* RENÉ FRAAYE

ABSTRACT. Diagenetically compressed ammonites from the Early Toarcian Posidonienschiefer in southern Germany yield new data on the diet and ingestion regulation of ammonites. About 4 per cent. of the relatively large body chambers of adult *Harpoceras falciferum* macroconchs contain distinctive food remains, mostly pereiopods of small decapod crustaceans, which probably were the main prey of this ammonite species, and rarely abdomens and telsons of the same crustaceans or aptychi of small ammonites. The contents of the digestive tract are preserved in the adapical three-quarters of the body chamber as a row of 'food balls'. The number of these food balls is variable; up to five have been counted. In most specimens it is not possible to distinguish between crop and stomach contents.

About 1 per cent. of adult *Harpoceras falciferum* macroconchs contain bivalve debris in their body chamber. Although in some specimens this may represent the crop content of the ammonite, in the majority of specimens the debris may be interpreted as food remains not of the ammonite itself, but of another animal living in the mantle cavity area of dead ammonites.

AMMONITES are one of the best documented fossil groups, with an extensive literature on morphology, evolution and palaeoecology. However, data on feeding mechanisms and diet are sparse. The aim of this paper is to give new informations about the diet of an important Early Jurassic species, *Harpoceras falciferum*, by investigation of the contents of the body chamber.

DIET AND FEEDING OF RECENT *NAUTILUS*

Today, most cephalopods are highly skilled carnivores, with a very efficient digestive system, the rate of ingestion ranging between three and 20 hours. The majority take a wide variety of prey: mainly crustaceans, molluscs and fishes and to a lesser extent echinoderms, polychaetes, chaetognaths and siphonophores. The prey may be ingested whole, or in bite-size pieces either including the exoskeleton or the flesh exclusively (Nixon 1987, 1988).

Modern *Nautilus*, which is similar to the ammonites in its exoskeleton and in many other respects, scavenges both exuviae and dead decapod crustaceans. Although *Nautilus* catches live prey when enclosed together in traps or aquariums, it has never been observed to catch live prey if this is able to escape. Different species of crustaceans are the main food source for *Nautilus* (Ward 1987, pp. 156–159). 'At every locale where crop contents or faecal residues have been examined, crustacean test fragments were recorded' (Saunders and Ward *in* Saunders and Landman 1987, p. 151). Ward and Wicksten (1980) identified 23 crustacean specimens (mostly *Aniculus aniculus*, a hermit pagurid crab, but also brachyuran and raninid crabs, a galatheid and fragments of a palinurid lobster, as well as fish bones) as crop, stomach, and intestine contents in nine specimens of *Nautilus macromphalus* from New Caledonia.

According to Nixon (1988, p. 645), *Nautilus* bites crustaceans 'into pieces of about 5 mm^3, which could pass along the highly distensible oesophagus (Haven 1972) to be stored in the large crop'.

Nautilus macromphalus from New Caledonia often eats fresh moults of larger crustaceans, such as lobsters (e.g. *Panulirus longipes*), Ward (1987, p. 159) referred to observations by Magnier and Laboute (1978) and Ward and Wicksten (1980). Ward (1987, p. 159) assumed that there are two

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THE DIET OF AMMONITES: PREVIOUS DATA

Stratigraphy and locality	Ammonite species	Crop and/or stomach content (interpretation by the original authors)	Author
Upper Jurassic (Lower Tithonian), lithographic limestone, Solnhofen area, Bavaria, Germany	*Neochetoceras steraspis* (Oppel)	Numerous small, broken aptychi, interpreted as brood	Michael (1894)
	Same specimen, plus a second, similar one	Ditto, interpreted as stomach content	Lehmann (1976, p. 129)
Upper Jurassic (Upper Kimmeridgian), lithographic limestone, Nusplingen, Baden-Württemberg, Germany	*Physodoceras* sp.	Stomach content: ossicles of the crinoid *Saccocoma* sp.	Lehmann (1976, p. 129)
	Same specimen	Crop content: echinoid spines	Riegraf *et al.* (1984, p. 58)
Lower Jurassic (Lower Toarcian), Posidonienschiefer, Haverlahwiese, Lower Saxony, Germany	*Hildoceras* (*Hildaites*) *levisoni* (Simpson)	Stomach content: jaw apparatus of a small ammonite	Lehmann and Weitschat (1973)
Posidonienschiefer, Unterer Schiefer, Dotternhausen, Baden-Württemberg, Germany	*Phylloceras heterophyllum* (J. Sowerby)	Crop content: debris of *Pseudomytiloides dubius* (J. de C. Sowerby), shells, and doubtful echinoderm remains	Riegraf *et al.* (1984, pp. 53–54, 57)
Posidonienschiefer, same locality	*Harpoceras falciferum* (J. Sowerby)	Crop content: doubtful debris of *Pseudomytiloides dubius*	Riegraf *et al.* (1984, p. 56)
Posidonienschiefer, Schierferklotz layer, Ohmden, Baden-Württemberg, Germany	*Hildoceras* (*Hildaites*) *serpentinum* (Reinecke)	Crop content: small aptychus	Riegraf *et al.* (1984, pp. 54–56)
Posidonienschiefer, Unterer Schiefer, Dotternhausen, Baden-Württemberg, Germany	*Hildoceras* (*Hildaites*) *levisoni* (Simpson)	Stomach content: calcitic debris resembling echinoderm stereom	Riegraf *et al.* (1984, p. 57, 189)
	A second specimen	Stomach content: aragonitic shell debris	Riegraf *et al.* (1984, p. 57)

[*continued on p.* 560

EXPLANATION OF PLATE 1

Figs 1–4. Distal parts of pereiopods with chelae of *Coleia*? sp. in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1, many chelae; W 60; × 1·6. 2, single chela; W 50; × 2·7. 3, many chelae; W 68; × 2·4. 4, single chela; W 63; × 2·8.

PLATE 1


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JÄGER and FRAAYE, body chamber contents of *Harpoceras*

THE DIET OF AMMONITES: PREVIOUS DATA (*Cont.*)

Stratigraphy and locality	Ammonite species	Crop and/or stomach content (interpretation by the original authors)	Author
Lower Jurassic, Sinemurium, ?Yorkshire, England	*Arnioceras* sp.	Stomach content: foraminifers and ostracods	Lehmann (1972)
Triassic, Spitzbergen	*Svalbardiceras spitzbergense* (Frebold)	Stomach content: many fragments of ostracods	Lehmann (1985, p. 102; 1990, p. 184)

main reasons why *Nautilus* ingests moults: to extract the protein from the extensive integuments which line the internal parts of the moults and/or the calcium for shell building.

Ingestion of lobster exuviae follows a specific pattern in which *Nautilus* consumes the exoskeleton beginning at the posteriormost part of the abdomen and continuing anteriorly (Ward and Wicksten 1980; Tshudy *et al.* 1989). In laboratory feeding experiments pereiopods are often seized first, with biting concentrated on the tips of the pleopods and the softer underside of the abdomen. When *Nautilus* reaches the telson, it eats the uropods and subsequently the abdomen segment by segment. The heavily calcified cephalothorax is left behind (Ward 1987, p. 159). On the other hand, Ward and Wicksten (1980) reported finding well-worn pieces of crustacean carapace material in the crop, stomach and caecum of *N. pompilius* from Fiji and *N. macromphalus* from New Caledonia. An adult *Nautilus* feeds on a large lobster exuvia for as long as two hours (aquarium experiment, Ward and Wicksten 1980).

Saunders and Ward (*in* Saunders and Landman 1987, p. 151) reported that the dissected crops of specimens of *N. pompilius* from Lae, Papua New Guinea, contained many fresh fragments of deep-water regular echinoids including both test fragments and viscera. Other specimens of *N. pompilius*, dissected in Manus, contained coleoid beaks, and occasional *Nautilus* tentacle fragments.

According to Ward (1987, pp. 159–160), *Nautilus* appears to be a windfall feeder. Ward *et al.* (1977) showed that a 500 g *Nautilus* can store up to 100 g of bait material in its crop. K. Mangold (pers. comm.) has conducted experiments on individuals of *N. macromphalus* showing that food material can be stored for up to two weeks in the crop before digestion. Tanabe *et al.* (1980) reported that the crop is capable of enormous enlargement, as it may measure as much as 80 mm long by 50 mm in diameter when filled with food.

An excellent summary was provided by Lehmann (1976); Lehmann (1990) did not refer to additional specimens, but (p. 185) wondered why no crustaceans (except for ostracods) were found in the crop or stomach contents of ammonites, especially as he thought that crustaceans were one of the main types of prey of ammonites.

Bandel (pers. comm., see Riegraf *et al.* 1984, p. 59) supposed that the food remains found inside ammonites may have come out of the stomach of fishes, which probably had been eaten by the ammonites.

EXPLANATION OF PLATE 2

Figs 1–5. Complete pereiopods with chelae of *Coleia*? sp. in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1–4, W-shaped pairs of pereiopods. 1, W 9; × 1·8. 2, W 20; × 1·5. 3, W 1; × 0·5. Arrow indicates section enlarged in fig. 4. 4, × 2·2. 5, V-shaped pereiopod; W 5; × 3·0.


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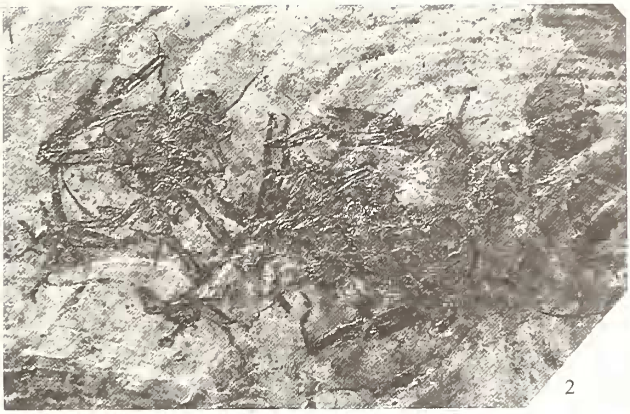
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JÄGER and FRAAYE, body chamber contents of *Harpoceras*

DIET OF AMMONITES FROM THE LOWER TOARCIAN OF DOTTERNHAUSEN

In the Early Toarcian Posidonienschiefer of south-west Germany compressed body chambers occasionally preserve contents of different kinds. A single large crustacean from Dotternhausen has recently been interpreted by Fraaye and Jäger (1995) to have occupied an empty body chamber.

Dark homogeneous spots in ammonites from Dotternhausen and other localities were figured and described as crop and stomach contents by Riegraf *et al.* (1984, pp. 53–59). Such brown or (less commonly) black spots are frequently found and are present also in some of the specimens described below. However, as they are often indistinct, they are not further considered here.

Ammonites are present at every level of the 9–10 m thick Posidonienschiefer facies in Dotternhausen, being common at most levels. Within a section a few decimetres thick, in the lowermost part of the *commune* subzone, above the 'Inoceramenbank', the intense red-brown colour of the periostracum is most attractive to the collector, and the recovery of complete specimens is relatively easy, as the shale often splits along bedding planes. In this part of the section collecting of ammonites has been much more intensive than in other parts of the sequence. Ammonite taxa collected from this layer are (in degree of abundance): *Dactylioceras commune*, *Harpoceras falciferum* (although being the index of the *falciferum* subzone, this species ranges into the *commune* subzone, the diameter of adult macroconchs here in general being 200–300 mm), *Hildoceras* ex gr. *douillei*/*sublevisoni*, *Pseudolioceras lythense*, *Phylloceras heterophyllum*, *Lytoceras* sp. and *Phymatoceras* cf. *escheri*.

From this part of the Dotternhausen section, 72 specimens with determinable body chamber contents are described and discussed, all being adult macroconchs of *Harpoceras falciferum*.

Remains of a small eryonid crustacean, possibly *Coleia* sp., were found in 62 ammonite specimens (Pls 1–4; Pl. 7, fig. 1; Pl. 8). Some of these have been previously reported by Jäger (1991, pp. 33–34, erroneously interpreted as inhabitants; 1993, p. 66, fig. 49). Two of the *Coleia*?-bearing specimens and nine more specimens contain concentrations of bivalve debris (Pls 5–6). A single specimen preserves several small aptychi, but neither crustacean remains nor bivalve debris, in its body chamber (Pl. 7, figs 2–4), and some of the specimens with crustaceans contain small aptychi as well (Pl. 7, fig. 1; Pl. 8). All fossils, unless stated otherwise, are housed in the collection of Rohrbach Zement in Dotternhausen.

Specimens with crustacean remains (Coleia? *sp.*)

In the part of the section described above, roughly 4 per cent. of adult *Harpoceras falciferum* macroconchs (estimated during excavation in the quarry: three out of 77 specimens) or even more in the lowermost part of the section (estimated from a later excavation without counting) preserve crustacean remains in their body chamber. In other co-occurring ammonite genera, crustacean remains are extremely rare; the few specimens will be described elsewhere. No crustaceans outside ammonite shells have been found. However, the 'inhabitant' *Palaeastacus*? described by Fraaye and Jäger (1995) comes from this level, and bite marks in some ammonite shells from the same layer (e.g. Jäger 1991, fig. 3) provide indirect evidence for the presence of large crustaceans. In specimens of *Harpoceras falciferum* from lower stratigraphical levels no crustaceans have been found.

EXPLANATION OF PLATE 3

Figs 1–4. Food balls including fragments of pereiopods, some of them with chelae, of *Coleia*? sp. in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. The broad chelae indicated by arrows (figs 1–2) may belong to a different genus. 1, W 4; ×2·2. 2, W 48; ×2·9. 3, W 3; ×2·4. 4, W 18; ×3·0.

PLATE 3


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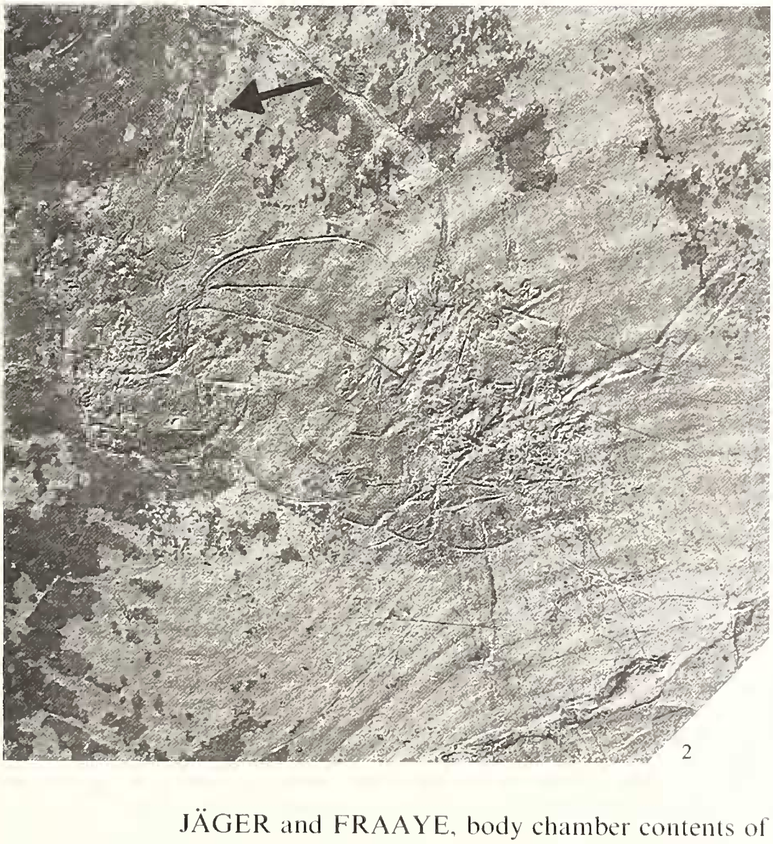
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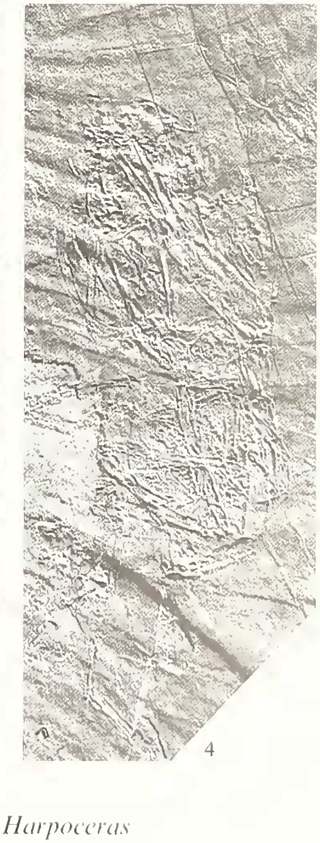
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JÄGER and FRAAYE, body chamber contents of *Harpoceras*

These observations allow the following conclusions to be drawn:

1. *Harpoceras falciferum*, like modern *Nautilus*, frequently fed upon crustaceans (dead or exuviae?), whereas representatives of other ammonite genera normally did not. This underscores suppositions of a number of authors that living conditions of various genera differed.
2. *Coleia*? must have lived in separate geographical regions (probably nearer to the coast, perhaps in Franconia, where crustaceans are more often found than in Swabia), and *Harpoceras falciferum* must have eaten them there and subsequently returned over some tens or even more than a hundred kilometres to the basin area around Dotternhausen.
3. As specimens of *Harpoceras falciferum* from lower strata do not preserve crustaceans inside their body chamber, either the preferred kind of food or the conditions of preservation of food remains must have changed.

In 54 of the 62 specimens with crustaceans, the body chamber is complete, or the region where the aptychi should be expected at least is preserved. Ten of these 54 specimens (= 18·5 per cent.) preserve aptychi. This is nearly the double percentage than in the total number of adult *Harpoceras falciferum* macroconchs with or without crustaceans from the same strata: only eight out of 77 *Harpoceras* specimens (= 10·4 per cent.) preserve their aptychi in the body chamber. Thus, in specimens without crustaceans, the contents of the body chamber has decayed to a greater extent than in specimens with crustaceans. This means that originally more than the mere 4 per cent. of *Harpoceras* had crustaceans in their digestive tract, and that many lost their digestive tract together with their aptychi during decay of the soft parts.

All crustaceans in *Harpoceras falciferum* body chambers (except for the *Palaeastacus*? described by Fraaye and Jäger 1995) are of comparable size, most specimens being similar to *Proeryon*, but distinctly smaller. Thus assignment to *Coleia* seems probable, although diagnostic features cannot be made out. However, it cannot be ruled out that they represent juveniles of *Proeryon* which lived near-shore.

Most *Coleia*? specimens are preserved as indistinct remains of pereiopods (Pl. 3, figs 1–4), and of distal parts of pereiopods with chelae (Pl. 1, figs 1–4; Pl. 4, fig. 2), but sometimes V-shaped complete pereiopods including chelae (Pl. 2, fig. 5) or even W-shaped pairs of pereiopods with chelae (Pl. 2, figs 1–4) are seen. Few chelae are broader than the others and may represent a different genus (Pl. 3, figs 1–2). Remains of the abdomen and telson (Pl. 4, figs 3–6) are much rarer than pereiopods. Not a single remain of the cephalothorax has been identified. This pattern is in full accordance with the pattern of selective consumption in Recent *Nautilus* described above. However, the complete pereiopods or pairs of pereiopods are much larger than the 5 mm^3 bites that Recent *Nautilus* manages. 'The hard, calcified cutting edges found on the jaws of *Nautilus* are used to break up hard crustacean carapace material; the very different jaw edge morphologies of the Jurassic ammonites so far studied suggests differences in food source' (Ward 1987, p. 248). Although this last conclusion is questioniable, *Harpoceras falciferum* at least was unable to bite the crustaceans into such small pieces.

Some questions, however, remain unresolved. For example, it is not quite clear yet if the aptychi were used for biting or as a 'shovel'. Dagys *et al.* (1989, pp. 49–50) suggested differences in the function of anaptychi and aptychi: 'The main distinguishing feature of the anaptychus-type lower jaw is absence of calcareous coverings and presence of a more or less marked pit in the rostral part

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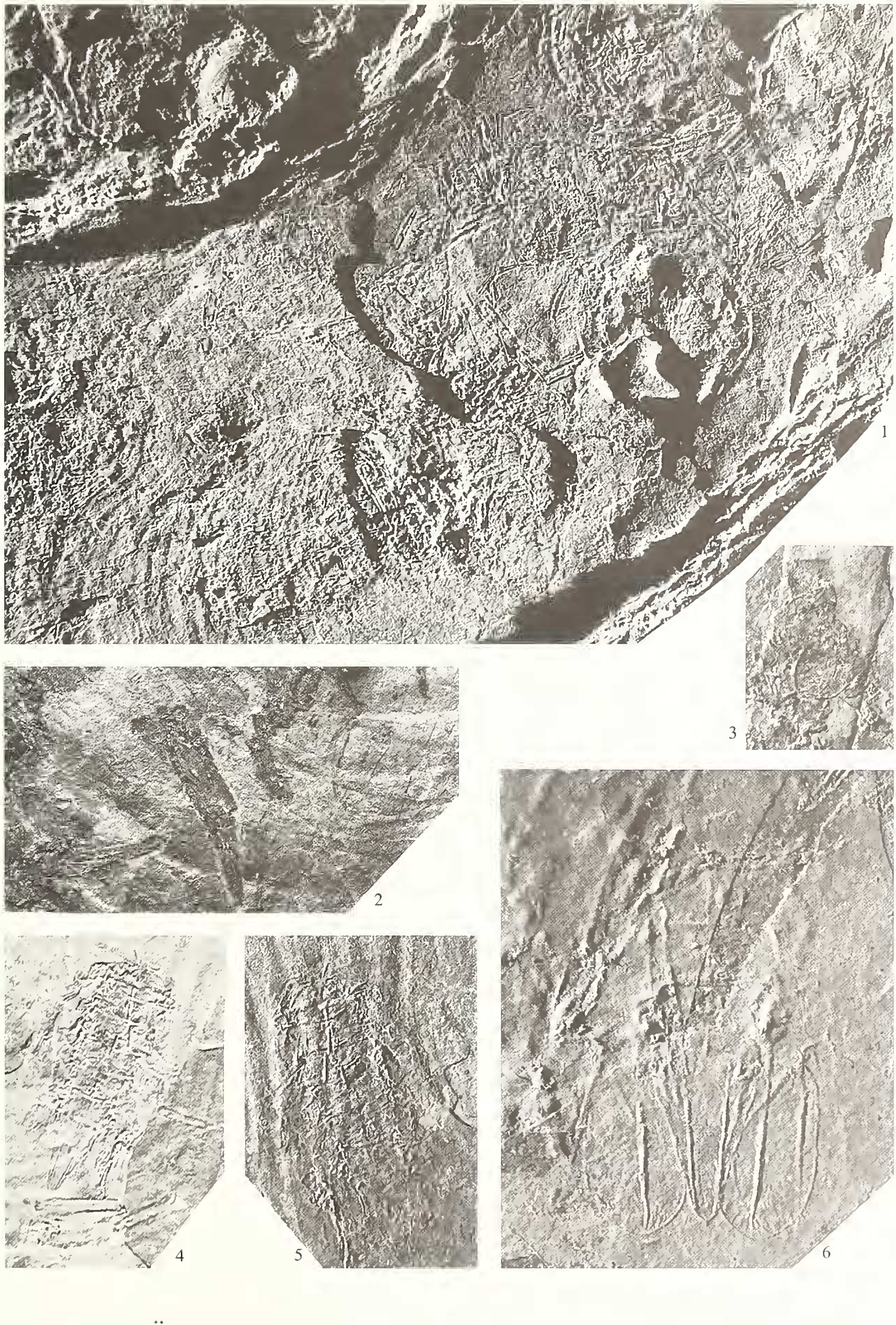
EXPLANATION OF PLATE 4

Figs 1–6. Remains of *Coleia*? sp. in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1, large masses of pereiopods; W 40; ×1·3. 2, fragments of pereiopods with chelae; W 27; ×2·6. 3–6, fragments of abdomen and telson. 3, W 17; ×4·6. 4, W 18; ×3·0. 5, negative impression of specimen in fig. 4; W 18; ×3·5. 6, W 62; ×4·6.

PLATE 4



JÄGER and FRAAYE, body chamber contents of *Harpoceras*

of the inner lamella. It is likely that the upper jaw was overlapped by the lower jaw, as in recent cephalopods, and that the pit represents the place of insertion of the rostrum of the upper jaw. If this reconstruction is correct, it may be supposed that the main action of this type of jaw apparatus was crushing. In this case the older ammonoids may have preferred rather coarse food and animals with fairly hard shells. This specialization was absent in the aptychus-type of jaw apparatus, which is characterized by the presence of calcareous plates covering the flanks of the lower jaw. Their front edges may have supported a cutting function of the jaw, at least more so than in the anaptychus type. But the earlier suggestion of a shovel-like function (Lehmann 1972, 1975, 1981), without too much crushing or cutting, still has its merits. Morton and Nixon (1987) suggested that the shovel-like lower jaws may have expelled water while retaining captured small prey.' If the aptychi acted as a 'shovel' only, how did *Harpoceras* manage to separate pereiopods from the cephalothorax?

It cannot be ruled out totally that the crustaceans were consumed not by the ammonite, but by an unknown post-mortem occupant of the empty ammonite shell. There are, however, arguments contradicting this alternative hypothesis.

1. One should expect that a hypothetical occupant should throw the aptychi out of the shell by its life activities rather than keep them inside. The fact is, however, that the aptychi are still present significantly more often in ammonites with crustaceans than in ammonites without crustaceans.
2. The fact that in Dotternhausen hitherto *Coleia*? has not been found in the slabs outside the ammonites, and thus presumably did not have its natural habitat at this locality, raises the question of how the crustaceans were transported from their habitat to Dotternhausen, if not by an actively swimming ammonite (if the ammonite was already dead and drifted passively only, one should expect the soft body including the aptychi and the crustaceans to decay quickly and to have fallen out of the shell.) It seems improbable that an unknown animal fed upon the crustaceans in their habitat, and then swam many kilometres to Dotternhausen to hide itself in an empty ammonite shell for digestion. In this case, the crustaceans should presumably be regarded as coprolites, but don't look like them. In the Posidonienschiefer, coprolites of carnivorous reptiles and fishes are usually preserved as three-dimensional yellow-brown phosphatic masses, whereas the ?coprolites of *Palaeastacus*? (Fraaye and Jäger 1995) are preserved as flattened circular spots.

The fact that *Coleia*? is not found outside the ammonite shells contradicts another hypothesis: that the crustaceans were only passively drifted into the ammonite shell by currents ('fossil trap'). There is no reason to believe that the potential of preservation of fossil crustaceans within the shell, which did not form a concretion, is greater than outside (in contrast to aragonitic gastropod shells, which are preserved only in certain calcareous concretions, but not in the shale outside).

Now that quite a number of specimens has been examined, the type of crustacean remains preserved, and the notable absence of the cephalothorax, clearly counters the hypothesis that the small *Coleia*? crustaceans either lived or moulted in empty ammonite shells (as erroneously supposed by Jäger 1991).

In some specimens the crustacean remains are distributed in no particular pattern in the body chamber, but more often they are concentrated in densely packed balls of varying shape and size. The normal diameter of these balls is 10–50 mm, but there are a few masses greater than 80 mm long and 50 mm wide with the crustacean remains lying in two or three different levels. Commonly, single pereiopods jut out of the compact balls. The single remains may be interpreted as being derived from disarticulated or partly disarticulated balls. When splitting up the slabs of shale, very often one part of a ball remains on one slab and the other part remains on the opposite slab, leaving a

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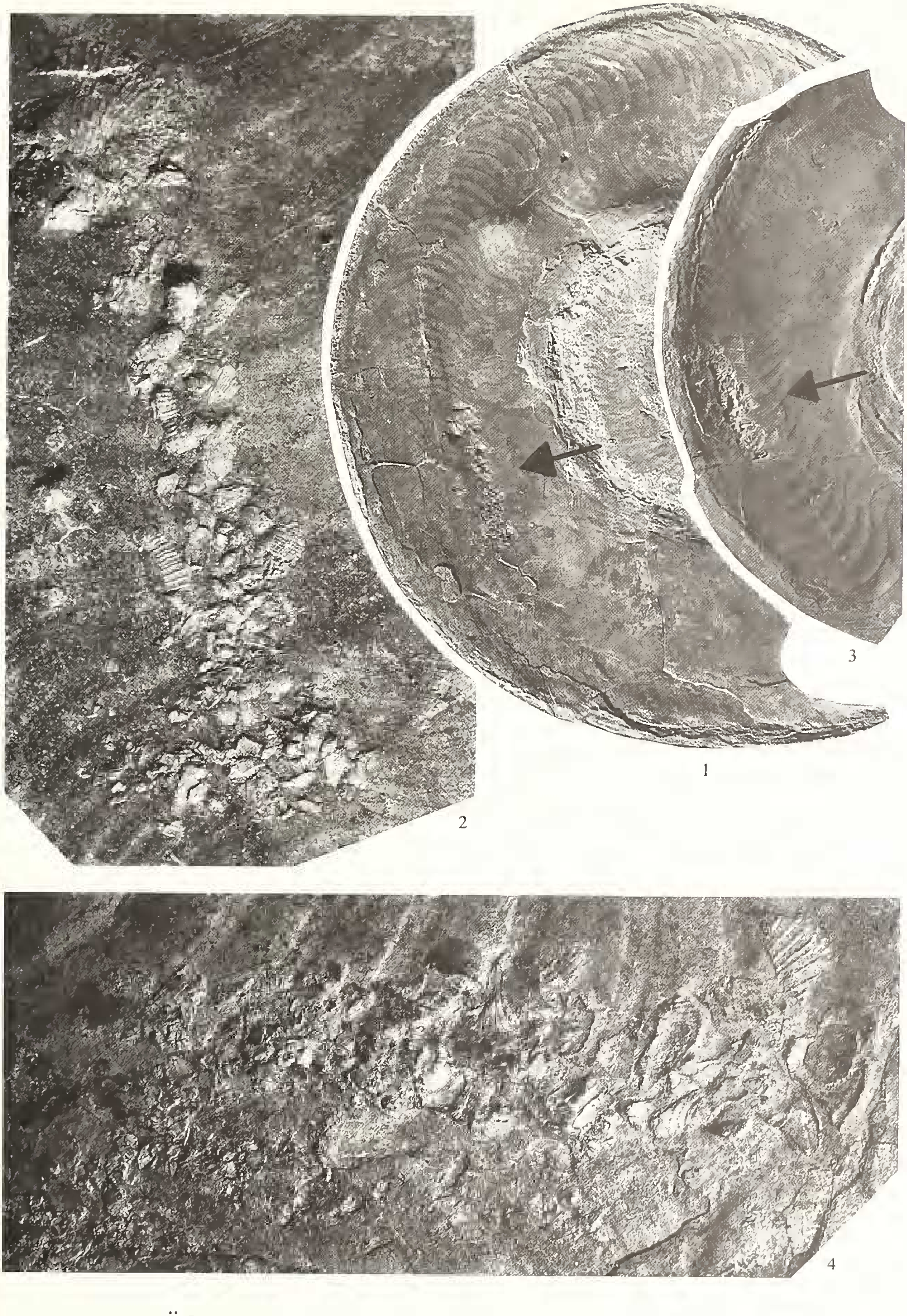
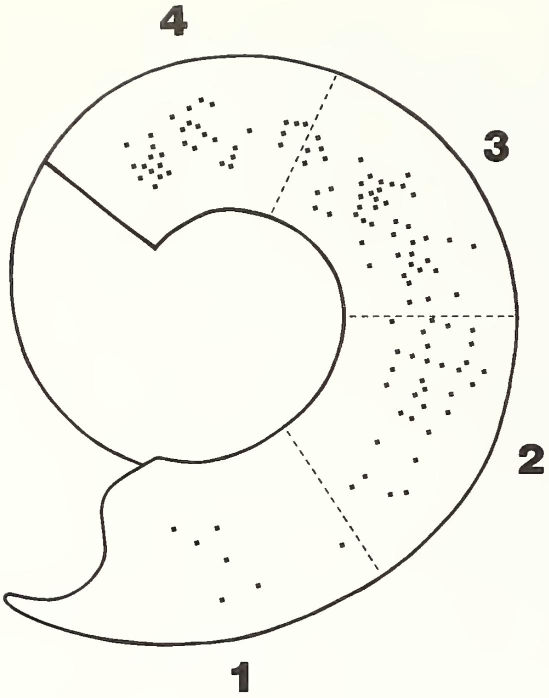
EXPLANATION OF PLATE 5

Figs 1–4. Bivalve debris in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1, W 55; the section enlarged in fig. 2 is indicated by an arrow; ×0·5. 2, ×2·5. 3, W 33; the section enlarged in fig. 4 is indicated by an arrow; ×0·5. 4, ×2·7.

PLATE 5



JÄGER and FRAAYE, body chamber contents of *Harpoceras*



TEXT-FIG. 1. Positions of centres of 120 food balls including *Coleia*? sp., in 58 *Harpoceras falciferum* specimens, drawn in the body chamber of an idealized ammonite.

complicated pattern of positive food ball fragments and negative impressions on either slab (Pl. 1, figs 1, 3; Pl. 3, figs 1, 3; Pl. 4, fig. 1). Some of the crustacean remains are fairly distinct when viewed under low-angle light, but others may be confused with compression cracks in the ammonite shell or are hidden under epizoans or broken away. Thus it is difficult to draw the correct circumference of the balls. Nevertheless, a sketch (Text-fig. 1) shows the position of the (approximate) centre of 120 food balls (seven more balls could not be located because the anterior and posterior ends of the body chamber are not preserved.)

The number of crustacean remains varies from a single pereiopod in the whole body chamber (Pl. 2, fig. 5) up to five crustacean balls plus several aptychi filling a considerable part of the body chamber (Pl. 7, fig. 1; Pl. 8, figs 1–3). This resembles the high storage potential of Recent *Nautilus* mentioned above. Counting of balls is difficult, because sometimes it is impossible to decide whether a large spot represents a single large ball or results from the close proximity of two partially disarticulated balls. Twenty-five specimens preserve a single ball, in 22 specimens there are two, in six specimens three, in five specimens four, and in four specimens five. In two exceptional specimens (registered as having four and five balls, respectively), masses of crustacean remains nearly fill the entire body chamber from the last septum to the aperture, leaving only small areas free (Pl. 4, fig. 1). This may even exceed the storage potential and casts doubt on the interpretation that all these masses were really consumed by the ammonite. One of these exceptional specimens does not preserve aptychi, but the other does. It may be a matter of chance that these two specimens both show bivalve encrustation.

EXPLANATION OF PLATE 6

Figs 1–5. Bivalve debris in the body chamber of adult macroconchs of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1, W 73; × 1·2. 2, W 30; × 1·7. 3, W 31; the section enlarged in figs 4–5 is indicated by an arrow; × 0·4. 4, × 1·3. 5, × 1·9.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JÄGER and FRAAYE, body chamber contents of *Harpoceras*

If the body chamber, whose length equals nearly three-quarters of a whorl in *Harpoceras falciferum*, is divided into four sectors of equal length from the aperture (sector 1) to the last septum (sector 4), then seven centres of food balls are positioned in sector 1, 32 in sector 2, 47 in sector 3, and 34 in sector 4. As there is only one position of maximum abundance (sector 3), it cannot be decided beyond doubt whether the crustacean remains represent crop contents (which should be positioned in sectors 2–3) and/or stomach contents (which should be positioned in sector 4). The remains in sector 1 and possibly those in the anterior half of sector 2, too, are assumed to have been dislocated, whereas the remains in the adapical three-quarters of the body chamber are preserved probably more or less in their original position in the digestive tract. The position of the digestive tract (oesophagus median, stomach in the posterior part (sector 4) of the body chamber) was shown in *Arnioceras* and *Hildoceras* by Lehmann (1972) and Lehmann and Weitschat (1973).

Specimens with bivalve debris

In the Posidonienschiefer, slabs very often show remains of *Pseudomytiloides dubius*, and other pseudoplanktonic bivalves of different species are often fixed to floating ammonite shells (Seilacher 1982). Due to the strong compression of both sediment and ammonites, it is sometimes difficult to decide whether the bivalves originally grew upon the ammonite shell or were washed into the empty ammonite by currents or eaten by the ammonite or occupant of the empty ammonite shell. Only in those cases where small bivalve fragments are concentrated within the ammonite body chamber may these in fact represent food remains.

In all 11 *Harpoceras* specimens, the bivalve debris forms but a single, usually longitudinal, rarely sub-circular, concentration 30–80 mm long and 20–40 mm wide in each specimen. The particle diameter is < 1–7 mm, rarely 10 mm. The fragments are mostly ribbed and originate either from *Pseudomytiloides dubius*, *Pseudomonotis substriata* (Münster), or *Oxytoma inaequivalvis* (J. Sowerby), well-preserved specimens of all three species being not rare within this horizon, and at least two of them had a pseudoplanktonic mode of life.

In contrast with the crustacean remains, bivalve debris concentrations are positioned in sector 2 in all 11 specimens, often close to the ventral side (Pl. 5, figs 3–4; Pl. 6, figs 3–5), less often to the ventro-median or median side (Pl. 5, figs 1–2; Pl. 6, fig. 1). This different pattern, together with the total absence of aptychi in all 11 specimens and the presence of large washed-in shells in some of the specimens, requires a different interpretation of the bivalve debris. Because of its position in the anterior part of the body chamber, it certainly does not represent the stomach contents of the ammonite. In some specimens it may be the crop contents, especially in one of the two specimens where the bivalve debris is associated with crustacean remains, showing that portions of the ammonite's soft parts were very probably still present in the body chamber. In the first specimen, the bivalve debris lies in between crustacean pereiopods, forming two balls in sector 2, median (crop content?). In the second specimen, it and the crustacean are found 70 mm apart. However, this is one of the few specimens where the food ball centres are positioned in sector 1 and probably are dislocated. In the other nine specimens with bivalve debris no crustacean remains occur.

EXPLANATION OF PLATE 7

Figs 1–4. Remains of *Coleia*? sp. and small aptychi in the body chamber of adult macroconchs of *Harpoceras falciferum* from the early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1, five food balls including remains of *Coleia*? sp., plus small aptychi outside the food balls. The ammonite's own large aptychus is also present. The sections enlarged in Pl. 8, figs 1–3 are indicated by frames. W 21 (now in collection of Geo Centrum Brabant, Boxtel); ×0·5. 2–4, two food balls including small aptychi, but no crustaceans. 2, W 35; the ammonite's large own aptychus is indicated by an arrow. The sections enlarged in figs 3–4 are indicated by frames; ×0·5. 3, ×2·5. 4, ×3·2.

JÄGER and FRAAYE, body chamber contents of *Harpoceras*

In the large ammonite *Phylloceras heterophyllum* (Sowerby) described and figured by Riegraf *et al.* (1984, p. 57, fig. 12) from the Unterer Schiefer of Dotternhausen, the shell debris of *Pseudomytiloides dubius* must represent crop content. In the *Harpoceras* specimens, however, the position of the bivalve debris probably reflects the position of the mantle cavity of the ammonite. As it seems improbable that a living ammonite was unable to remove debris from its mantle cavity, it may be that the debris was accumulated by a different animal (maybe crustacean, 'decapod kitchen') living in the mantle cavity of a dead ammonite.

The presence of soft parts in the dorsal region of the body chamber of the ammonite is needed to explain why the bivalve debris often is in a distinctly ventral position, although the ammonite was certainly buried lying flat on the sea-floor: in an empty body chamber the relatively heavy (in comparison with the crustacean remains) bivalve debris should flow to a median or even dorsal position, even if it was originally amassed in the ventralmost position at a time when the ammonite shell rested in a vertical position on the sea-floor.

Specimens with small aptychi

Aptychi much smaller than the aptychi of the ammonite in whose body chamber they are found are present in several of the *Harpoceras falciferum* with or without crustaceans, for example in a specimen with five crustacean balls (Pl. 7, fig. 1; Pl. 8, figs 1–3). If the small aptychi are complete, it cannot be determined whether they were eaten prey or were washed into the body chamber, for the body chamber often serves as a sediment trap containing complete ammonite shells up to several tens of millimetres in diameter. However, at least for a single *Harpoceras* specimen (Pl. 7, figs 2–4), it appears that the small broken aptychi inside the body chamber come from prey either eaten by the ammonite (more probable) or by an occupant of the empty ammonite shell (less probable). It is an adult macroconch which preserves its large aptychus in the body chamber. There are two balls in sector 3 median: one contains three, the other at least nine small aptychi; the length of small aptychi is 3–10 mm, and of its own large aptychi 50 mm. Most small aptychi are complete; some, especially the 10 mm specimen, are somewhat broken. The balls also contain two siphuncles of ammonites of 3 and 5 mm diameter, as well as fine-grained detritus.

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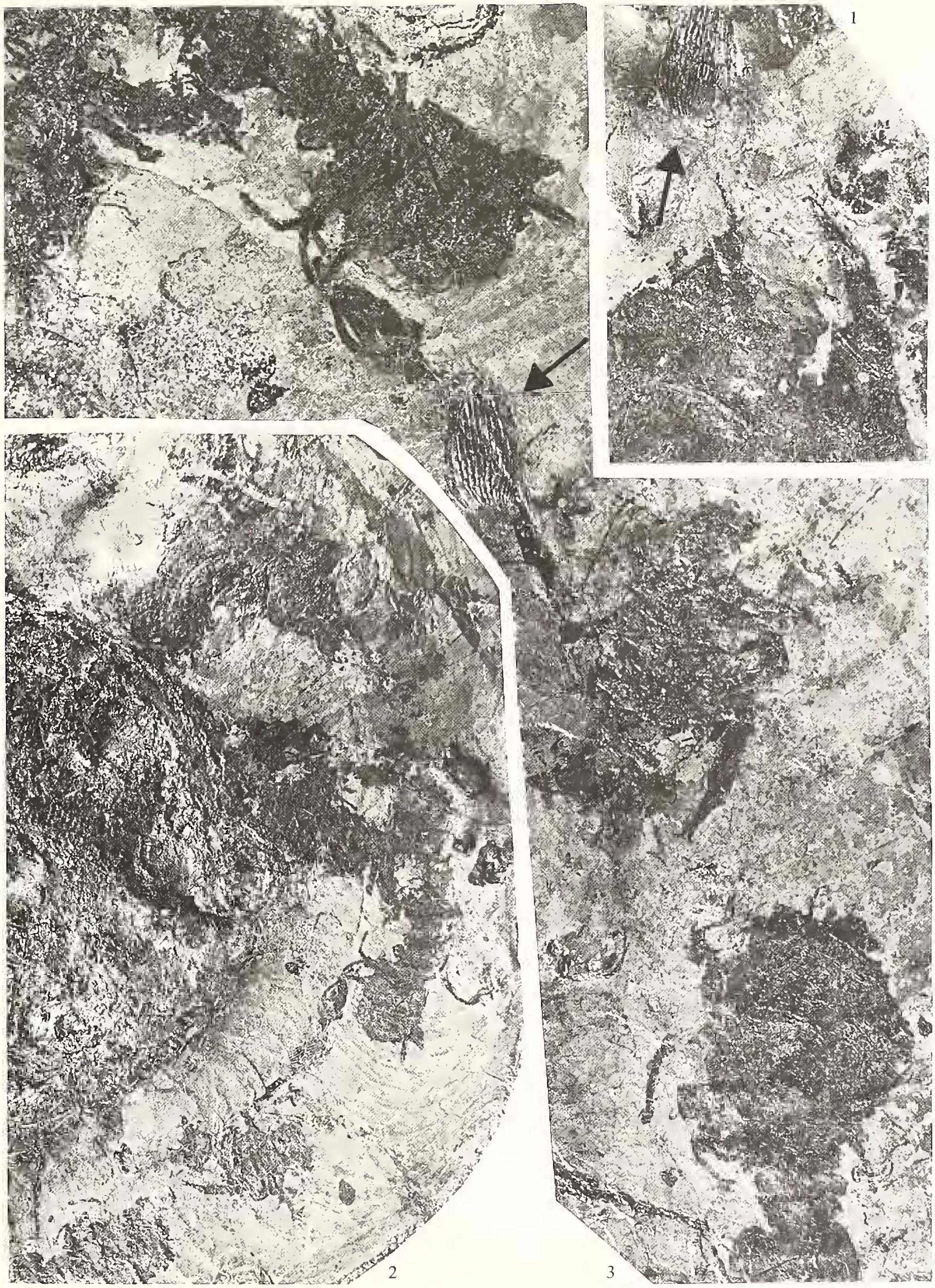
EXPLANATION OF PLATE 8

Figs 1–3. Five food balls including remains of *Coleia*? sp., plus small aptychi outside the food balls in the body chamber of an adult macroconch of *Harpoceras falciferum* from the Early Toarcian *commune* Subzone of Dotternhausen in south-west Germany. 1–3, W 21 (same specimen as Pl. 7, fig. 1, now in collection of Geo Centrum Brabant, Boxtel); arrows indicate small aptychi. 1, ×0·8; 2, ×2·0; 3, ×2·0.



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